12.—Further studies of the polymorphic species Crinia insignifera Moore (Anura, Leptodactylidae) on Rottnest Island

by A. R. Main*

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Abstract

Three populations of the polymorphic *Crinia insignifera* Moore on Rottnest Island have been studied from 1959 to 1964. Over the period of the observations the seasonal rainfall pattern has gone from dry to wet and during the same period the proportion of adults in the population has declined. Also during the warm dry 1959 and mild dry 1961 winters there was a poor survival of adults of the lyrate morph and a good survival of the ridged morph. However, during the years of observation, the morph frequency among recruits was constant from year to year.

Introduction

The present observations are a continuation of those reported earlier (Main, 1961) on the polymorphic frog, *Crinia insignifera* Moore. The earlier observations have been extended so that intra- and inter-locality comparisons of polymorph frequency and juvenile recruitment are possible. The observations presented cover the years from 1959 to 1964 inclusive which by good fortune encompass extremes of seasonal heat, cold, and drought. Localities mentioned in the text are shown on the map in Hodgkin and Sheard (1959).

Description of swamps sampled

Bagdad soak

An extensive area of freshwater seepage occurs on the western end of Lake Bagdad where ground water derived from sand dunes to the west of Lake Bagdad seeps out above a fossil shell bed which in this area forms the beach and bed of the lake. Passing away from the lake are found zones of vegetation as follows; a close cropped mat of *Sporobolus virginicus* which is heavily grazed by the quokka (*Setonix brachyurus* Quoy and Gaimard) at all seasons; then an area dominated by closely grown tussocks of the sedge, *Gahnia trifida,* which merges to the landward into an arid steppe of *Stipa, Poa* and *Acanthocarpus preissii.* Within the *Gahnia* zone there is a small depression about 10 feet long by 7 feet wide which contains water only during the winter (May to August) and at other times is grown over with *Sporobolus virginicus.* No *Gahnia* occurs in this depression. During the summer frogs of the genus *Crinia* can be located beneath the *Gahnia* tussocks adjacent to this depression. In years of heavy rainfall the soak does not increase its area but overflows into the adjacent lake.

* Zoology Department, University of Western Australia, Nedlands, Western Australia.

Negri soak

Lake Negri is a small salt lake to the west of Bagdad from which it is separated by a low sandy area. The shore of the lake is vegetated by *Salicornia, Gahnid* and *Sporobolus, Scirpus nodosus* and then the *Stipa-Poa* steppe.

During 1960, while searching for road building material, the Rottnest Board of Control excavated a small depression in the *Gahnia* zone on the northern edge of Lake Negri. The depression is about 15 feet square and up to 12 inches deep, and surrounded by the *Gahnia* tussocks both standing and uprooted. In the winter of 1960 this depression filled with rainwater and in it a small breeding congress of frogs established itself. It is presumed that the stock of this colony was derived from the population of a small seep in the *Gahnia* on the northwest side of Negri. In seasons of high rainfall the pond floods the adjacent lake shore. In the very wet year of 1963 the lake level rose and the flooded depression and saline lake became confluent with the consequent death of all tadpoles and most adults.

Lighthouse swamp

This is an area of peaty soil in an interdune depression not associated with salt lakes. The area is vegetated by *Arthrocnemum spp., Salicornia australis, Gahnia trifida* and *Sporobolus virginicus.* During the winter the depression is covered with water of varying depth and *Crinia insignifera* breeds throughout the swamp wherever the water is shallow. In exceptionally wet years the water level rises and floods the lower parts of the surrounding *Stipa-Poa* grassland. During the dry season of the year frogs can only be obtained from beneath stones among a grazed area of *Sporobolus* on the northern part of the swamp which passes to the north into sand dunes and coastal limestone vegetated with *Stipa, Poa* and *Acanthocarpus.*

Sampling and measurement

As in the earlier study samples were taken twice yearly: at post-breeding in November and at pre-breeding in March. At Lighthouse swamp samples were obtained by turning all the stones on the northern part of the swamp. These stones were carefully replaced after sampling. At Bagdad soak the standing and dead Gahnia tussocks adjacent to the depression were searched and a similar method was adopted at Negri. One sample was taken in June 1960 from a breeding congress on Lighthouse swamp at night by using a head-torch. Snout to vent

length measurements were made with vernier callipers while holding the frog on a flat surface. The phenotype of the frog was recorded at the time snout-vent measurement was made.

Results

Size distribution in samples

Breeding commences each winter in May or June and young frogs are metamorphosing by late August to mid-September as the ponds are drying. These young frogs feed and grow throughout the late spring and summer as rain showers permit them to forage from their hiding places.

Size distribution of breeding or sexually mature animals are shown in the upper histogram of Figure 1. This figure also shows the distribution by sex of animals caught in Lighthouse swamp in June 1960. In this situation males were calling, and females were either gravid with eggs, in oviduct, clasped and egg-laying, or spent. The size distribution can be taken as indicating sexual maturity at about 20 mm snout-vent length. The distribution also shows that females tend to be larger than males.

The size distribution of the post-breeding sample is shown in the lower histograms of Figure 1. This sample is clearly bi-modal. From the sample taken in June 1960 it is clear that the right hand group are sexually mature while the left hand group are immature and probably the progeny of the June breeding. This histogram also shows the size distribution of animals marked in November 1959 or March 1960 and recaptured in November 1960. It is noticeable that none of these recaptures are below the minimal length of sexual maturity established by the June 1960 sample. Collections made during the following years produced no case in which animals marked as juveniles in November or March were below 20 mm snout-vent length when recaptured the next November.

A number of egg masses were raised in artificial outdoor ponds within the Zoology department yards on the mainland. In these, development to metamorphosis was slower but subsequent growth and mortality appeared to be comparable to that in field situations. Progressive snout-vent length measurements of these animals are as follows: December 1, 1960—mean 9.3 mm, range 7.9 to 12.4 mm; January 31, 1961—mean 14.3 mm, range 10.9 to 16.4 mm; March; 15, 1961—mean 17.9 mm, range 16.9 to 18.6 mm. This rearing trial suggests that sexually mature frogs could be obtained twelve months after egg laying.

Field recaptures of individually marked animals from all three localities supports the above interpretation. However, frogs over 21 mm snout-vent length show very irregular growth and it was concluded that once an animal attains maturity it cannot be aged on size alone. Consequently, age distribution of the post-breeding samples has been restricted to juveniles, that is offspring of most recent breeding ($<$ 20 mm) and adults, that is more than one year old ($>$ 20 mm). This recognition of recruits as distinct from adults does offer increased opportunities in analysing genetic and age composition of population through a series of years.

Mortality and longevity

The heavy field mortality precluded establishment of detailed survivorship curves. For example in November 1961 on Lighthouse swamp 312 juveniles were individually marked. The following November a sample of 151 frogs yielded 22 adults of which only 4 were of the series of 312 juveniles marked the previous year. Recoveries were much higher in the early years. These have not been plotted because there is so much difference between the early and later years; a fact reflected in the change in numbers of adults and juveniles in the population (Tables 2, 3 and 4).

The longest recorded period for an individual survival at each locality was: Lighthouse swamp, 2 years, marked as adult November 1960 recaptured November 1962; Bagdad soak, 2½ years, marked as juvenile November 1961, recaptured March 1964; Negri soak, 2½ years, marked as juvenile November 1960, recaptured March 1963.

Population size

Population estimates. These have been made by the method in Main (1961), except in 1964 when simple recapture data were used to calculate population estimates by means of a Lincoln index. The results are shown in Table 1.

TABLE 1

Estimates of size of post-breeding papulations of C. insignifera at three swamps on Rottnest Island.

Year	Lighthouse	Bagdad	Negri
1955	1,021	....	....
1959	261	....	....
1960	330	337	189
1961	580	....	165
1962	702	....	817
1963	....	....	....
1964	1,341	....	....

Errors in method of making estimates. In dry seasons disturbed frogs retreat to secure hiding places and so are not caught. Also, in dry seasons there is not a good admixture of marked and unmarked animals and therefore there is a tendency to get spurious population estimates. November 1962 was a dry period, while the November 1961 sampling period was overcast and with dew each night. During the November 1964 sampling period light rain showers were common. The census in 1955 (Main, 1961) followed an exceptionally wet season and somewhat similar wet conditions prevailed during 1964. There is every reason to believe that the high estimates of these years truly represent the population size.

Age structure

The specimens have been categorised into adult and juvenile using the snout-vent lengths determined in Figure 1. Data are presented in Tables 2, 3 and 4.

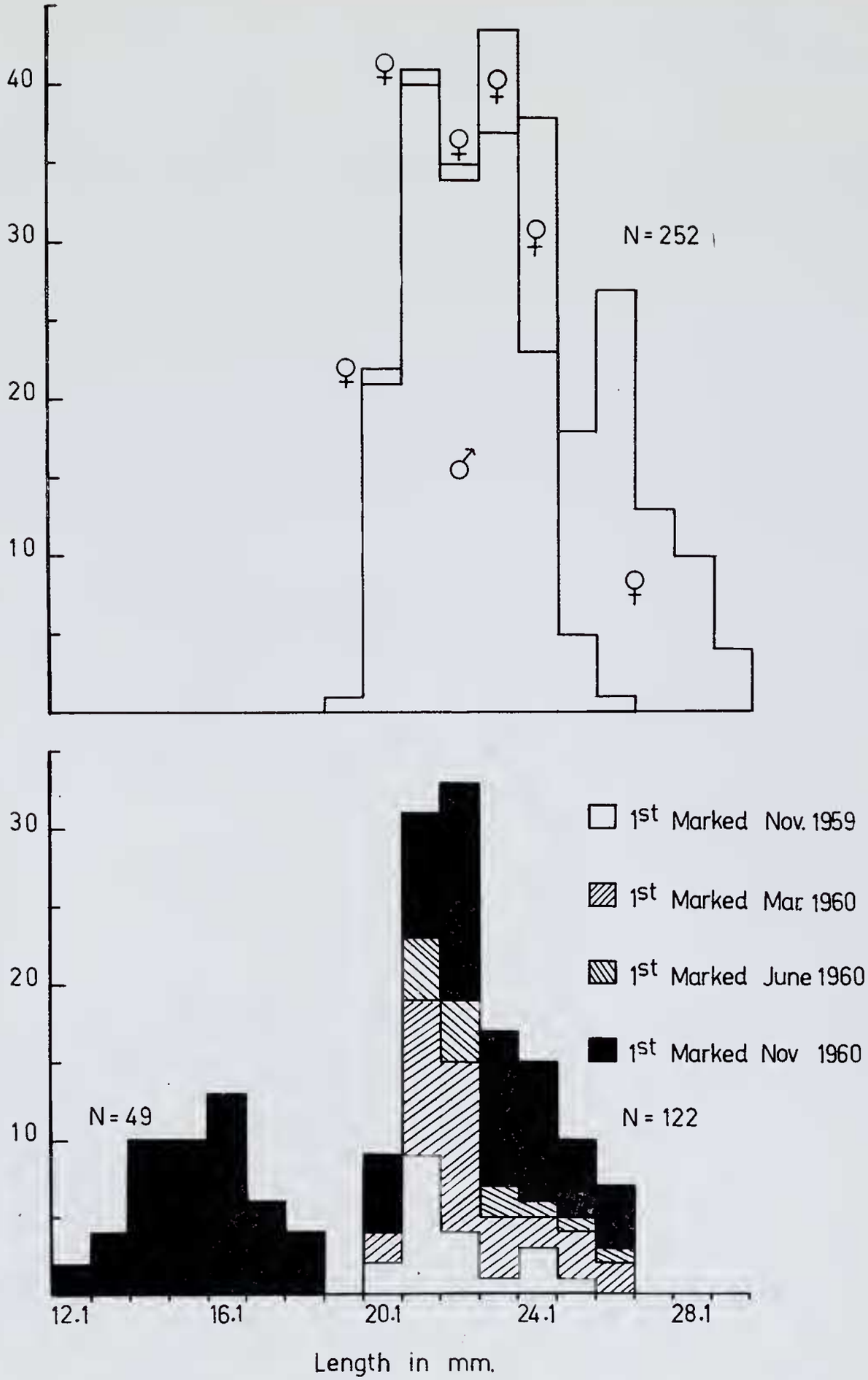

Figure 1.—Histograms of snout vent measurements of two samples of *Crinia insignifera* collected from Lighthouse soak, Rottnest Island. Upper. Sample collected June, 1960. Lower. Sample collected November, 1960.

Annual changes within localities

All November samples from each locality show a pattern characterised by greater adult frequency in the earlier years and greater juvenile frequency in later years. These changes are most marked in the Lighthouse swamp and Negri soak populations in which the differences are statistically highly significant (Lighthouse swamp $p < 0.001$, Negri soak $p > 0.001, < 0.01$), at least pronounced at Bagdad soak. These differences reflect changes in adult survival and recruitment, particularly as each of these contributes to the population structure; survival was good in the early years and recruitment poor, later the adult survival was poor and recruitment relatively good. While the foregoing is true for the series of observations, comparison of each observation with the preceding one shows that at Lighthouse swamp statistical significance in the proportion of juveniles to adults is reached between November 1960 to November 1961, and again between November 1962 and 1963. At Negri soak statistical significance in the proportion of juveniles to adults is reached between November 1960 to November 1961, p almost 0.02 and November 1962 $p < 0.01$. Tests are not possible on the full Bagdad soak series.

Inter-population comparisons

Comparisons are only possible for the three years 1960 to 1962. The differences between November 1960 samples from Lighthouse and Negri are highly significant ($p < 0.001$). In 1961 the differences between Lighthouse swamp and Bagdad soak are highly significant ($p < 0.001$, but the differences between Lighthouse swamp and Negri soak are not significant. In 1962 Lighthouse swamp and Negri soak are not different but each is significantly different from Bagdad soak ($p < 0.001$).

In 1963 no sample was taken from Bagdad soak and the Negri soak population was catastrophically reduced by salt water flooding. In 1964 the Negri soak population was still very small. The Bagdad soak population was not estimated, but juveniles were common, while the Lighthouse swamp population was very large and dominated by juveniles.

Genetic composition of populations

Lighthouse swamp. The data are presented in Table 2. A statistical analysis of these results shows:

Total population. A change in frequency of morphs between November 1959 and November 1960 ($p < 0.05 > 0.02$) with no statistically significant change subsequently.

Recruitment. There is no statistically significant difference between recruitment from year to year.

Differential survival of frogs. The age categories developed suggest that the March sample is comparable with the adults of the following November. Comparison shows November 1959 adults to differ significantly from the March 1959 sample (p almost 0.001, χ^2 10.22) but other samples are not significantly different.

Bagdad soak. The data are presented in Table 3. A statistical analysis of these results shows:

Total population. There is no statistically significant difference in morph frequencies in the samples over the years.

Recruitment. There is no difference in morph frequencies among recruits from year to year.

Differential survival of frogs. There is a significant difference in frequency of morphs present between March 1961 and adults November 1961 (chi square 4.268 $p < 0.05, > 0.02$).

Negri soak. The data are presented in Table 4. A statistical analysis of these results shows:

Total population. There is no significant difference in morph frequencies present from year to year.

TABLE 2

Lighthouse Soak; composition of population samples by phenotype and age.

Year and Month	Composition by Phenotype		Composition by Age and Phenotype				Composition by Age	
			Adult		Juvenile			
	Ridged	Lyrate	Ridged	Lyrate	Ridged	Lyrate	Adult	Juvenile
1959—								
March	49	50	....	....	....	....	....	....
November	54	25	38	11	16	14	49	30
1960—								
March	41	24	....	....	....	....	....	....
November	90	81	63	59	27	22	122	49
1961—								
March	22	24	....	....	....	....	....	....
November	206	178	45	27	161	151	72	312
1962—								
March	34	30	....	....	....	....	....	....
November	85	66	12	10	73	56	22	129
1963—								
March	36	36	....	....	....	....	....	....
November	127	98	3	3	124	95	6	219
1964—								
March	13	7	....	....	....	....	....	....
November	375	270	11	9	364	261	20	625

TABLE 3

Bagdad Soak; composition of population samples by phenotype and age.

Year and Month	Composition by Phenotype		Composition by Age and Phenotype				Composition by Age	
			Adult		Juvenile			
	Ridged	Lyrate	Ridged	Lyrate	Ridged	Lyrate	Adult	Juvenile
1960—								
March	44	48	..	....	....	....	....	....
November	33	32	33	30	....	2	63	2
1961—								
March	61	61	....	....	....	....	....	....
November	51	32	34	16	17	16	50	33
1962—								
March ...	45	38	....	....	....	....	....	....
November	12	5	7	3	5	2	10	7
1963—								
March	....	....	....	....	....	....	....	...
November	2	1	....	....	....	....	....	....
1964—								
March	22	12	....	....	....	....	....	....
November	16	9	2	1	14	8	3	22

TABLE 4

Negri Soak; composition of population samples by phenotype and age.

Year and Month	Composition by Phenotype		Composition by Age and Phenotype				Composition by Age	
			Adult		Juvenile			
	Ridged	Lyrate	Ridged	Lyrate	Ridged	Lyrate	Adult	Juvenile
1960—								
March	....	....	....	....	....	....	....	....
November	24	21	11	7	13	14	18	27
1961—								
March	35	16	....	....	....	....	....	...
November	54	34	14	5	40	30	19	70
1962—								
March	13	5	....	....	....	....	....	...
November	48	31	3	3	45	28	6	73
1963—								
March	17	3	....	....	....	....	....	
November	....	2	....	....	....	....	2	
1964—								
March	....	....	....	....	....	....	....	..
November	2	....	1	1	1	1	2	2

Recruitment. There is no difference in morph frequencies among the recruits in the years 1960 to 1962.

Differential survival of frogs. There is no statistical difference in morphs present between March 1961 and November 1961 adults.

Intra-population comparisons

Total populations. All populations are statistically similar from year to year with respect to frequency of morphs present.

Recruitment. All populations are similar with respect to frequency of morphs present among recruits.

Differential survival of frogs. The November 1961 samples from all populations show a decline in the lyrate morph compared with the previous March. Only in the case of Bagdad soak does this reach statistical significance. However, when the March and November samples from the three localities are pooled, the large sample does show the change to be significant almost at the p = .02 level (chi square 4.80). This suggests that the decline in frequency of lyrate animals is real and not an artefact of sampling.

Discussion

Earlier (Main, 1961) I attempted to explain the differences in morph frequency between the pre- and post-breeding samples in 1959 as follows;

> "The advantage enjoyed by the ridged morph may be due to:
>
> (a) More rapid development so that, as larvae, ridged animals may take advantage of more ephemeral waters in dry years.
>
> (b) The larvae of the morph may be able to tolerate the warmer temperatures which are found in warm dry seasons."

The earlier information was interpreted in the absence of a distinction between the contributions of recruitment and adult survival to the total morph frequency. Ability to distinguish juveniles of the recent breeding from older animals in a post-breeding sample now allows another interpretation which can be considered after reviewing the results presented above.

Classification of the November samples into recruits and adults has exposed the threefold nature of the problem viz.:—

Constancy of phenotypes in recruitment; changes in survival among frogs of one phenotype in two seasons (1959; 1961); domination

of total population by juveniles towards the end of the study period. It is of interest to see whether any of the observed changes in the populations can be related in any way to the different seral stages present at each locality and/or the different seasonal weather pattern over the years of the study.

Ecological succession

Of the three localities described earlier Negri soak is clearly earliest in the succession, no rotting litter has accumulated and the water is still alkaline. On the other hand Bagdad soak is nearest the climax, especially with respect to surrounding sedges. The data suggest that seral stage only has an effect on population structure insofar as at Bagdad soak the decline in adult frequency is delayed compared with the other two sites.

Seasonal weather pattern

The seasonal weather for the years 1959 to 1964 has been summarised in Table 5. The seasons have varied from warm dry (1959) to cold dry (1960) mild dry (1961) to mild wet (1963). Over this range of environmental conditions there has been no statistically significant change in the proportion of phenotypes present among the recruits.

TABLE 5

Perth weather, May to September, years 1959 to 1964 inclusive.

Year	Temperature Average Deviation from Mean (°F.)	Rain-days Deviation from Mean (days)	Sunshine Deviation from Mean (hours)	Rainfall Deviation from Mean (inches)
1959	+ 2·2	— 9	+ 66	— 10
1960	— 1·9	— 4	+ 81	— 6
1961	+ 1·1	— 12	+ 80	— 4
1962	+ 1·4	+ 3	....	— 4
1963	+ 1·1	+ 25	— 155	+ 4·5
1964	+ 0·24	+ 9	+ 3·0	+ 3·28

In the warm dry 1959 season there was a significantly poorer survival of the lyrate animals at Lighthouse (the only place then under observation). Again in the mild dry 1961 season the data are suggestive that lyrate survival is poorer in all localities. When data of all localities are pooled the decline is significant almost at the p = .02 level. It thus appears that lyrate adults are less able to stand warm winter conditions than ridged animals.

Conclusions

Over the period of the observations the seasonal rainfall pattern has gone from dry to wet and during the same period the proportion of adults in the populations has also declined. These changes are statistically most marked at Negri soak and Lighthouse swamp. The explanations of these observations appear to lie in a combination of, habitat preferences of adult frog, seral stage and minor local topographic conditions. *Crinia insignifera* is a frog which can only persist in swamps or marshes that are dry during the summer. During winter time they enter water to breed, but at other times leave the water and occupy adjacent marshy, but not flooded parts such as the *Gahnia* zone surrounding Bagdad soak. It so happens that the Bagdad soak is the only one in which flooding of the adjacent sedges does not take place in wet years. Here, so to speak, the adults are never flooded out into the inhospitable and unsuitable grassland and it is here that the survival of adults appears best. In the other localities adults are driven into unsuitable habitats by flooding in wet years and this is reflected in the declining proportion of adults in population samples as the years become wetter.

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